

Notes on the Family Lekythoporidae (Bryozoa, Cheilostomata)

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Introduction

(a) *Cheilostome Ovicells*

In recent years, several kinds of cheilostome ovicell have been investigated, and the origins and relationships of the various body wall layers involved have been traced through ontogeny. As a result, it has become obvious that the ovicell, which may be regarded as all the walls defining and protecting the brood chamber and the contained embryo, has several very different origins. Ovicells may be derived wholly, or in part, from diverticula of terminal walls or from extensions of frontal walls and, or, frontal shields. They may be derived wholly, or in part, from one or more zooids. They may be modified, interzooidal, frontally budded kenozooids, or may be formed from one or more kenozooids budded from the maternal zooid, which produces the ovum, or from a sequentially distal zooid or zooids (see Cook, 1979 for brief review). The general term 'ovicell' may therefore be defined functionally, but not morphologically, and it appears that the protective coverings for brood chambers have often been evolved convergently and show only superficial similarities.

All ovicells which have been investigated in detail, and all those which may be inferred by inspection to have analogous ontogeny, are 'distal' in position to the opening edge of the operculum of the maternal zooid. Generally, this 'distal' orientation is also the same as the direction of budding of zooids 'away from' the ancestrula as the colony develops. Even in colonies with 'reversed frontal budding' (where the distal part of the orifice is directed towards the ancestrular region, see below), the opening of the ovicell is placed close to the orifice of the maternal zooid, on that side of the operculum which opens to allow protrusion of the lophophore (see Cook & Lagaij, 1976). This position is correlated with the position of the coelomopore through which the ovum passes to the exterior. In all cheilostomes which have been investigated, the coelomopore is placed at the base of the 'distal' pair of tentacles. Passage of ova into ovicells is achieved by protrusion of the lophophore and apposition of the coelomopore to the ovicell orifice (see Silén, 1945).

Proximally placed ovisacs, which are principally uncalcified have been reported in the anaskan genus *Aetea*, but their ontogeny may be intussusceptive and quite unlike that of other known ovicells (Cook, 1977). Proximal calcified ovicells have also been described in several cheilostome ascophoran genera, which were grouped together in the family Lekythoporidae by Levinsen (1909), and further reviewed by Canu & Bassler (1929). The reported occurrence of 'proximal' ovicells infers that the position of the coelomopore, or at least the behaviour of the maternal lophophore, is radically different from all other cheilostomes in only one group, the Lekythoporidae. Such a difference would be fundamental, although it could be postulated for the genus *Inversiula* (Microporellidae), which is apparently equally aberrant, and where the operculum is hinged distally (see

Moyano, 1972). The brood sac in *Inversiula* is an interior diverticulum of part of the cuticular outer body wall (tentacle sheath) housed in specially enlarged brooding zooids. The operculum is orientated almost vertically, which would apparently allow passage of ova from a partially protruded lophophore into the ovisac in the 'normal' manner. This has never been observed in living specimens, but Nielsen (1981) has described passage of ova into ovicells closed by the operculum, in which the lophophore was not protruded, but was dimorphic, with very short tentacles.

The hingeing of the operculum in the Lekythoporidae is not like that of *Inversiula* and investigation of specimens of the five genera attributed to the family shows that the ovicell is placed in the 'normal' distal position with respect to the orifice, but that the pattern of astogeny is one of 'reversed frontal budding'. The modifications in zooidal morphology resulting from this type of growth are described below.

(b) Frontal budding and colonial and zooidal morphology

Frontal budding is a common phenomenon only in cryptocystidean ascophorans, although it occurs sporadically, in a modified form, initiating overgrowths in umbonuloid ascophorans and some anascans. In some cryptocystidean ascophorans, columns of successive, frontally budded zooids may occur (see Banta, 1972, fig. 1 (1), 3). Each zooidal element arises as an intussusceptive expansion of frontal cuticle, with underlying epidermis, of the primary zooid of the series. These together form the boundary wall of an expansion of hypostegal coelom, which is presumed to be provided with nutrients from the visceral coelom by means of the marginal frontal septulae in the frontal calcified shield. As the cuticle-covered bud reaches its full size, a secondary cryptocystidean frontal shield, also with marginal septulae, grows into, and partitions, its coelom into visceral and hypostegal elements. Cryptocystidean frontal shields are interior walls (see Boardman & Cheetham, 1973), and because there is communication between hypostegal and visceral coeloms, these zooids have the potential to form successive series of frontally budded members vertically to the horizontal plane of the primary zooids. Functionally, frontally budded zooids may be regarded as being identical to primary zooids budded through septulae in distal or lateral walls; but morphologically, they may also be regarded as extensions only of the originating primary zooid, because they have no basal walls. An even more integrated kind of frontal budding is found where more than one primary zooid contributes to the development of more than one frontal bud. These interzooidal frontal buds may form nodular masses or erect branches, and are sometimes composed of groups of integrated polymorphic zooids with differing functions (e.g. *Hippoporidra*, see Cook, 1983). Frontally budded zooids frequently have morphologies and orientations different from those of the primary series (see Boardman *et al.*, 1969, fig. 5), and apart from not possessing basal walls, often have no recognisable lateral walls.

In some minute, globular colonies, all budding is frontal, and the position and orientation of the zooids is rigidly patterned and 'reversed' with respect to the direction of growth. In these forms, the distal side of the orifice, the side on which the operculum opens, is directed towards, not away from the ancestrular area, as it is in 'normal' colony growth. In addition, all the calcified walls may be regarded as frontal shields, which consist of a 'concealed' portion, from which new frontal buds arise, and an 'exposed' portion which surrounds the orifice (see Cook & Lagaaij, 1976). Combinations of 'normal' and 'reversed' orientations of frontal buds occur in the genus *Sphaeropora* (see Cook & Chimonides, 1981).

In the Lekythoporidae all colonies are known or inferred to have minute, encrusting bases. In *Lekythopora* and *Poecilopora* zooids are budded distally from the ancestrula for only one or two astogenetic generations. The rest of the colony is composed of erect branches of frontally budded zooids, each of which is orientated with the distal edge of the orifice towards the outer face of the branch. Each zooid bud arises interzooidally from more than one zooid of the earlier astogenetic generation and develops a cryptocystidean frontal shield with numerous frontal septulae. Fully formed zooids are vase-shaped or columnar and all the vertical calcified walls (whether axial or peripheral) form one continuous 'frontal' shield.

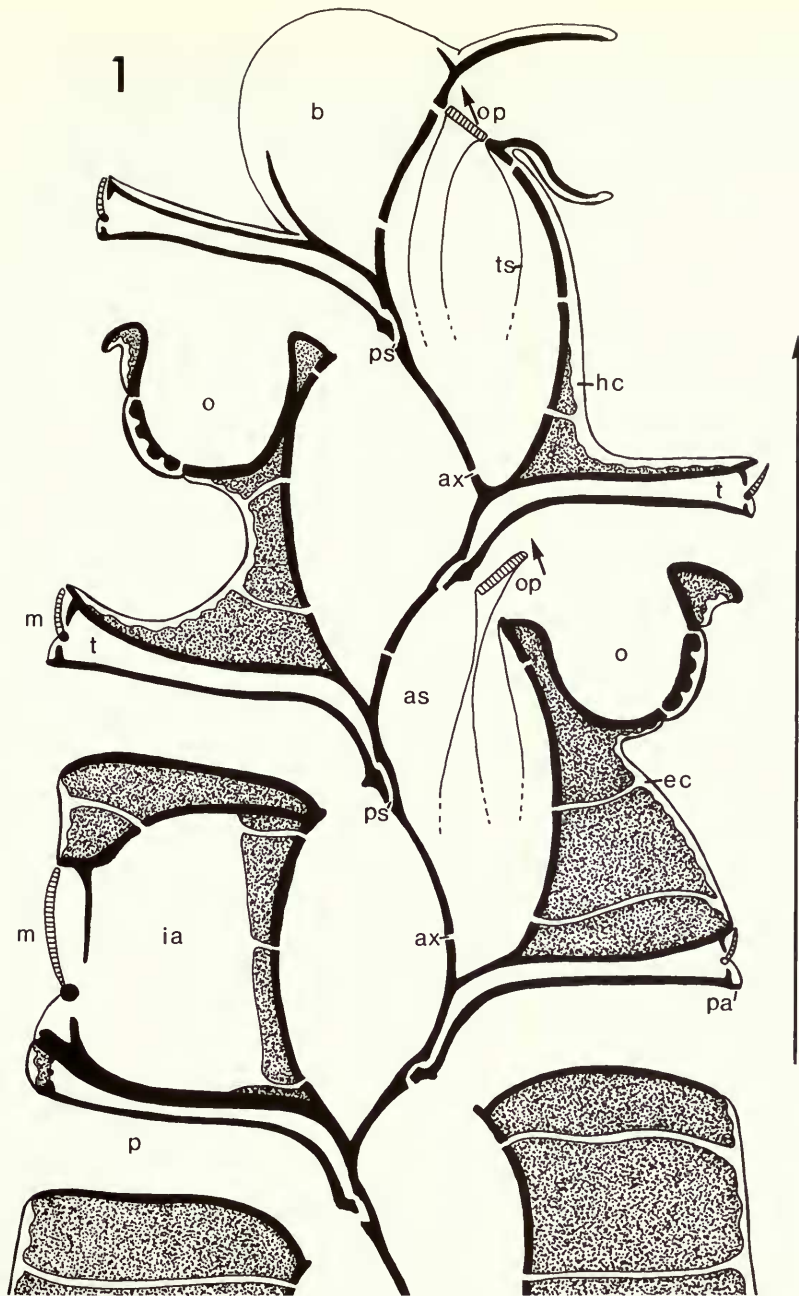
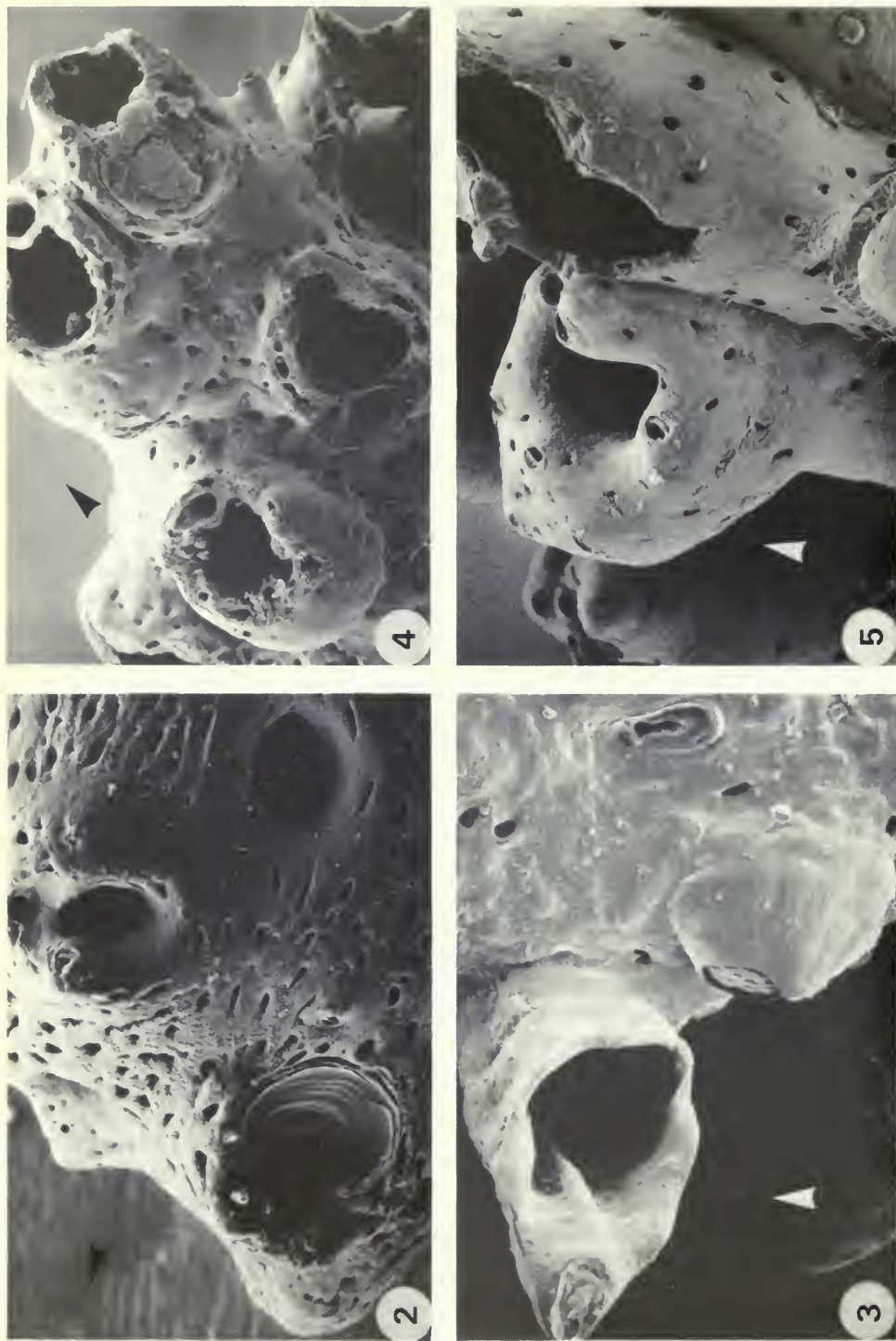


Fig. 1 Diagrammatic, idealised longitudinal section through axis of an erect branch of Lekythoporidae (based on *Lekythopora* and *Poecilopora*). Direction of colony growth (astogenetically distal), arrow at right. External cuticles only shown (thin lines); Primary calcification (thick lines); secondary and extrazoooidal calcification stippled; *as* ascus; *ax* axial frontal septulae; *b* topographically distal, frontal bud; *ec* extrazoooidal coelom (derived from amalgamation of hypostegal coelom of several zooids); *hc* hypostegal coelom; *ia* interzoooidal, frontally budded avicularium; *m* mandible; *o* brood chamber within peristomial ovicell; *op* operculum (direction of opening arrowed); *p* peristome; *pa* peristomial avicularium; *ps* peristomial frontal septula; *t* tube connecting peristomial avicularium with frontal septula; *ts* tentacle sheath.



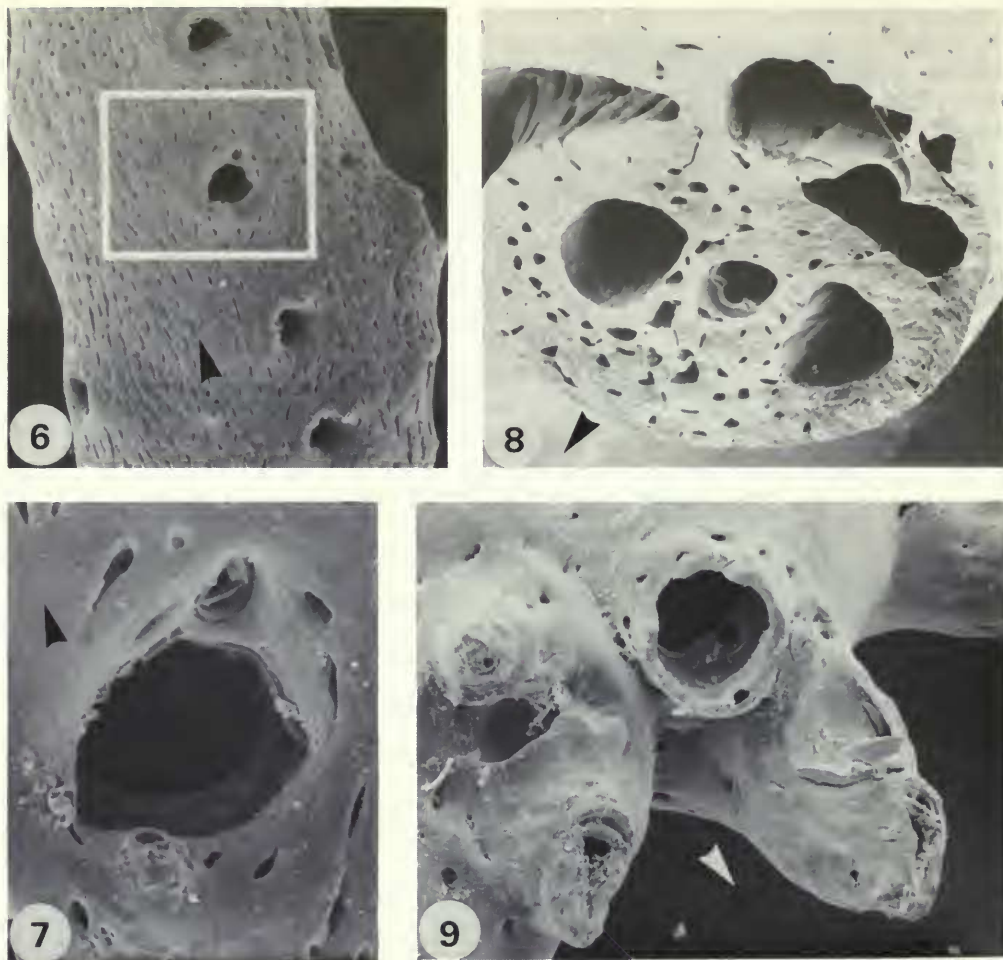
Figs 2-5 Scanning electron micrographs of ovicells of Leukthoporidae; arrows indicate direction of colony growth: (2) *Catadysus immersum* (Busk) BMNH 1963.2.12.247, Montevideo, growing tip with developing ovicell (left) and complete ovicell (right). Note rapid extrazoooidal thickening of frontal shields and slit-like frontal pores $\times 80$; (3) *Poecilopora anomala* MacGillivray BMNH 1888.11.14.291, Port Phillip Heads, marginal zooid with elongated peristome and terminal avicularium (left) and ovicell with frontal area $\times 200$; (4) *Turritigera stellata* (Busk) BMNH 1897.12.9.520B, Montevideo, growing tip with developing ovicell (right) and complete ovicell (left) $\times 90$; (5) *Orthoporida solid* (Busk) BMNH 1899.7.1.3525, S.W. Australia, ovicell with avicularia $\times 57$.

Septulae are present in the axially directed 'concealed' part of the shield, and in the outwardly directed part. This, together with the circumoral region forms the equivalent of the 'exposed' part of the frontal shield in conescharelliniform colonies with 'reversed frontal' budding (see Cook & Lagaaij, 1976, and Fig. 1). One or more circles of septulae surround the primary orifice. The septulae allow the expansion of hypostegal coelom axially to form new zooid buds, and peripherally to allow thickening of the exposed frontal shield calcification and, or, the budding of peristomial or interzooidal avicularia and kenozooids. The primary orifice is terminal, and is orientated with the proximal edge of the operculum directed axially and in a more 'distal' position, with respect to the direction of growth of the branch, than the outwardly directed (morphologically) distal edge (see Fig. 1). This is because the longitudinal axes of the zooids are curved towards the outside of the branch. The peristome arises as a ridge between the circum-oral septulae and other frontal septulae. It becomes tubular and often very elongated, continuing the outward curve of the zooid axis. The ovicell is an expanded diverticulum on the peripheral, morphologically distal, side of the peristome, but the curvature of the zooid and peristome is such that it appears to be topographically 'proximal' in position (see Fig. 1). This illusion is completed in several species when the peristome develops a small secondary 'sinus' on its astogenetically distal, but topographically proximal side (Fig. 18).

The problem of interpreting the relationships of the primary orifice and the ovicell is exacerbated by the length of the peristome and by the rapid development of secondary calcification and frontally budded kenozooids in most species. The hypostegal coeloms may even amalgamate, with the breakdown of interzooidal cuticle, and form extrazooidal coelom with massive extrazooidal calcification. The presence of septulae and extension of hypostegal coelom on the outer sides of the peristome also assists this calcification. The exposed frontal shields, peristome and even ovicells sometimes become completely obscured within only two astogenetic generations of the growing edge or tip of the branch (Fig. 2).

Longitudinal and transverse sections reveal details of the relationships of zooid budding and communication, but because most zooidal axes are curved in more than one plane, complete axial sections cannot be obtained. In colonies with regularly cylindrical branches, *Catadysis*, or irregular cylindrical extensions, *Lekythopora* and *Orthoporidra*, all zooid orifices are orientated with their proximal edges pointing axially and nearly vertically, i.e. in the direction of growth. In colonies which appear superficially to be composed of two 'laminae' of zooids, *Poecilopora*, the proximal sides of orifices of one 'lamina' are directed towards those of the opposing 'lamina', in the same manner as those of the erect, but rooted genus *Flabellopora* (see Harmer, 1957). In colonies with rounded branches with one 'frontal' surface, *Turritigera*, the zooidal axes are twisted as well as curved, but the proximal edges of the orifices are directed towards the axis of the branch. The 'basal' side of these colonies is entirely composed of extrazooidal calcification (Fig. 8).

Avicularia occur on the edge of the peristome in all species. They are derived from circum-oral frontal septulae, and one proximo-lateral avicularium at least is always present, although several may occur. A long, tubular connection between the avicularian chamber and the originating septula passes through the peristomial calcification. This often traces a curved path, which perhaps reflects the distortions in zooidal axes which occur during calcification of the bud. Sometimes the avicularia are raised on long hollow processes, which may bear small secondary avicularia laterally as well as terminally. The long processes become obscured during later thickening, leaving the avicularia at the surface of the branch, where they may appear to be frontally budded interzooids. In addition, large frontally budded, interzooidal avicularia also develop later in astogeny, especially at the bases of branches. The apparently 'confused' budding pattern (especially in *Lekythopora* and *Orthoporidra*), and the effects of extrazooidal calcification therefore make it difficult to distinguish the origins of avicularian types except near the growing tips. Similar difficulties in the genus *Turbicellepora* have been described by Hayward (1978), who also discussed the descriptive terminology applicable to the large 'spatulate' avicularian rostra which often occur in 'celleporine' forms. Measurements of zooids are also difficult to define and obtain, because



Figs 6–9 Scanning electron micrographs of orifices of Lekythoporidae; arrows indicate direction of colony growth: (6) *Catadysis immersum* (Busk) BMNH 1963.2.12.247, Montevideo, part of branch showing secondary orifices and frontal pores $\times 26$; (7) *C. immersum*, secondary orifice with avicularia. Note astogenetically distal (topographically proximal) edge of primary orifice at lower level $\times 130$; (8) *Turritigera reticulata* sp. nov. BMNH 1890.4.16.2A, Marion Island, broken edge of branch from distal side showing one primary orifice (centre), zooid cavities, and thick 'basal' extrazoooidal calcification of branch $\times 57$; (9) *T. fenestella* sp. nov. BMNH 1890.4.16.2B, Marion Island, detail of zooid at branch tip, showing sinuate primary orifice, secondary orifice and large avicularium $\times 112$.

the shape of zooids is often irregular, the primary orifice is completely hidden and secondary calcification obscures all limits of structures. One measure of the relative length of zooids may be the distance between the centres of secondary orifices in distal series, but this is very susceptible to error if peristomes are worn or broken. Opercula and primary orifices may often be visible in broken branches, and examination from the topographically 'proximal' (zooid interior) side may reveal differences in shape between them.

Systematic Section
LEKYTHOPORIDAE Levinsen

Lekythoporidae Levinsen, 1909 : 89, 383.

TYPE GENUS. *Lekythopora* MacGillivray.

DESCRIPTION. The characters of the family are redefined as follows. Colonies erect or semi-erect, arising from a small encrusting base which becomes strengthened by frontally budded kenozooids, avicularia and, or, extrazoooidal calcification later in astogeny. All zooids of the secondary zone of change and repetition (see Boardman *et al.*, 1969) are frontally and interzoooidally budded. Zooids columnar, with a centrally placed, terminal primary orifice. Proximal sides of orifices and asci orientated towards the central axis of the branch. All vertical calcified walls formed as an interior, cryptocystidean shield; axial part concealed, peripheral part and circum-oral region exposed. Shield with a hypostegal coelom and frontal septulae, some of which form a circum-oral ring. Primary calcified orifice straight, curved or sinuate proximally, surrounded by a raised, tubular peristome. Avicularia arising from circum-oral septulae, occasionally numerous, always one proximo-laterally, which appears to be topographically distal. Subrostral chambers terminal, on the edge of the peristome or a mucronate process arising from the peristome. Rostra acute or rounded, mandible slung on a complete bar. Subrostral chamber connected to the originating septula by a long tube, which passes through the calcified wall of the peristome. Interzoooidal, frontally budded avicularia sporadic, variously orientated, mandible slung on a complete bar, which may bear a ligula. Brood chamber protected by a large, globular peristomial ovicell, sometimes with an exposed, frontal cuticular area, or with pores and small avicularia on its surface.

REMARKS. The family has been defined (e.g. by Bassler, 1953) to include the genera *Lekythopora* MacGillivray, *Poecilopora* MacGillivray, *Turritigera* Busk, *Catadysis* Canu & Bassler, *Orthoporidra* Canu & Bassler and *Actisecos* Canu & Bassler. Of these, all but *Actisecos* have been described as having 'proximal' ovicells. *Actisecos*, a rooted, lunulitiform genus, has little in common with the other genera and was assigned to the family Actisecidae by Harmer (1957 : 854). The remaining genera differ from each other principally in details of budding pattern, the shape of the primary orifice and operculum, and the characters of avicularia and ovicells.

Most of the specimens examined are small, rarely more than 10–15 mm in height, and type material is often worn and fragmentary. A few colonies, *C. immersum*, *O. compacta*, *T. reticulata* and *T. fenestella*, are relatively large and exceed 50 mm in height or width. Some species show distinct substratum preferences. *Lekythopora* is often found on erect hornerid and adeonid bryozoans, *Poecilopora* on flexible cellariiform and cellulariiform bryozoans or on hydroids, *Turritigera* is often associated with other bryozoans or with polychaete tubes, and colonies of *Orthoporidra* may originate on small stones.

With one exception, *Poecilopora cribritheca*, all species are from the Southern hemisphere, and perhaps apart from *Lekythopora*, are from fairly deep, sometimes very deep, cold waters. Generally, bottom temperatures have been given only for Antarctic localities in published data, and those for low latitude, 'tropical' and 'subtropical' specimens are not known (see Table 2). Several Antarctic species have been reported as abundant, but material examined here, from the Zoological Museum Amsterdam (ZMAC), the National Museum of Victoria (NMV), the British Museum (BMNH), and the Manchester Museum (MM) collections, is not generally plentiful. In view of the enormous, but unworked collections which have been made from the Antarctic shelf, and the increasing number of species becoming known from deep waters, it should be possible, theoretically at least, to obtain larger quantities of some of the species described here, and to analyse their population variation in colony form and zooidal morphology. Several species appear to belong to complexes, composed of widely distributed populations, each with different character correlations. Additional information on early astogeny, and internal features such as tentacle

Table 1 Average measurements of zooids of Lekythoporidae (in mm)

	Lz	lz	Lpo	lpo	Lov	lov
<i>L. hystrix</i>	0.70	0.40	0.12	0.11	0.20	0.40
<i>P. anomala</i>	0.40	0.28	0.08	0.07	0.15	0.20
<i>P. cribritheca</i>	0.50	0.30	0.12	0.11	0.18	0.20
<i>T. stellata</i> Stn 320	0.50	0.30	0.13	0.16	0.20	0.25
<i>T. stellata</i> Stn 142	0.60	0.35	0.13	0.18	0.25	0.35
<i>T. reticulata</i>	1.20	0.50	0.13	0.11	0.40	0.50
<i>T. fenestella</i>	0.75	0.35	0.17	0.12	0.25	0.30
<i>C. immersum</i>	0.65	0.50	0.12	0.17	0.25	0.35
<i>O. compacta</i>	0.80	0.50	0.19	0.23	0.40	0.50
<i>O. solida</i>	1.20	0.50	0.20	0.25	0.40	0.50
<i>O. petiolatus</i>	0.60	0.33	0.12	0.13	0.24	0.30

Table 2 Nominal Recent records of Lekythoporidae and *Orthoporidae*. Additional temperature data from Murray, 1895 and Livingstone, 1928; estimated depths and temperatures in parentheses

Species	Locality data	Latitude	Longitude	Depth (metres)	Temperature (°C)	Reference
Lekythoporidae						
<i>L. hystrix</i>	Port Phillip Heads	38°30'S	144°30'E	(60)	(+17)	BMNH
<i>L. hystrix</i>	Port Western	38°30'S	145°30'E			BMNH
<i>L. hystrix</i>	Port Jackson	34°S	151°E	(60)	(+17)	BMNH
<i>L. avicularis</i>	Port Jackson	34°S	151°E	146	(+17)	Maplestone 1909
<i>P. anomala</i>	Port Phillip Heads	38°30'S	144°30'E	(60)	(+17)	BMNH
<i>P. anomala</i>	Twofold Bay	36°59'S	150°20'S	275	(+12.8)	BMNH
<i>P. anomala</i>	Maria Island	42°37'S	148°E	73		Thornely 1924
<i>P. cribritheca</i>	Sulu Archipelago	6°8'N	121°19'E	275	(+12)	Harmer 1957
<i>T. stellata</i>	Montevideo	37°17'S	53°52'W	1100	+2.8	Busk 1884
<i>T. stellata</i>	Cape of Good Hope	35°04'S	18°37'E	275	+8.3	Busk 1884
<i>T. stellata</i>	Cape Horn	53°S	68°W			Waters 1905
<i>T. stellata</i>	Is. Topar	50°8.5'S	74°41'W	360		Moyano 1974
<i>T. stellata</i>	Caleta Hale	47°57'S	74°41'W	40-50		Moyano 1974
<i>T. stellata</i>	Bellinghausen Sea	70°S	80°48'W	2500	+0.9	Waters 1904
<i>T. stellata</i>	Bellinghausen Sea	70°20'S	83°23'W	459	+0.8	Waters 1904
<i>T. stellata</i>	Bellinghausen Sea	70°15'S	84°6'W	659	+0.8	Waters 1904
<i>T. stellata</i>	Bellinghausen Sea	70°23'S	82°47'W	480	+0.8	Waters 1904
<i>T. stellata</i>	Bellinghausen Sea	71°14'S	89°14'W	460	-0.3	Waters 1904
<i>T. stellata</i>	Bellinghausen Sea	71°18'S	88°2'W	435	-0.3	Waters 1904
<i>T. reticulata</i>	Marion Island	38°S	46°40'W			BMNH
<i>T. fenestella</i>	Marion Island	38°S	46°40'W			BMNH

Continued

Species	Locality data	Latitude	Longitude	Depth (metres)	Temperature (°C)	Reference
<i>T. spectabilis</i>	Uruguay	36°49'S 38°16.9'S 36°55.7'S	53°15.4'W 51°56.1'W 53°01.4'W	1661-1679 4382-4402 2707		d'Hondt 1981 d'Hondt 1981 d'Hondt 1981
<i>C. immersum</i>	Montevideo	37°17'S	53°52'W	1100	+2.8	Busk 1884
<i>C. immersum</i>	Burdwood Bank	54°25'S	57°32'W	103		Hayward 1980
<i>O. compacta</i>	Bellinghausen Sea	70°S	80°48'W	2500	+0.9	Waters 1904
<i>O. compacta</i>	Bellinghausen Sea	71°18'S	88°02'W	435	-0.3	Waters 1904
<i>O. compacta</i>	Bellinghausen Sea	71°19'S	87°37'W	436	-0.2	Waters 1904
<i>O. compacta</i>	Halley Bay	75°31'S	26°36'W			BMNH
<i>O. compacta</i>	Scotia Bay	61°S	45°W			BMNH
<i>O. compacta</i>	McMurdo Sound	77°05'S	164°17'E	256		BMNH
<i>O. compacta?</i>	South Chile	62°28.5'S	59°41.5'W	119		BMNH
<i>O. compacta?</i>	Queen Maude Land	70°19.4'S to 70°20.9'S	24°12.6'E to 24°13.4'E			Redier 1965
<i>O. setosa</i>	Commonwealth Bay	64°32'S	97°20'E	201		Thornely 1924
<i>O. setosa</i>	Commonwealth Bay	66°08'S	94°17'E	220		Thornely 1924
<i>O. setosa</i>	Adelie Land	66°55'S	145°21'E	782	+1.8	Thornely 1924
<i>O. setosa</i>	Adelie Land	66°32'S	141°39'E	287	+1.62	Thornely 1924
<i>O. setosa</i>	Graham Land	65°S	64°W	750		Vigeland 1952
<i>O. setosa</i>	Graham Land	65°S	64°W	90		Vigeland 1952
<i>O. setosa</i>	Graham Land	65°S	64°W	140		Vigeland 1952
<i>O. petiolata</i>	Cape Horn	53°13'S	68°31'W	97	+6.6	Waters 1905
<i>O. petiolata</i>	Burdwood Bank	54°25'S	57°32'W	103		Hayward 1980
<i>O. petiolata</i>	Houtjes Bay	34°10'S	18°10'E			BMNH
<i>O. solida</i>	S. W. Australia	42°42'S	134°10'E	4758	+1.1	Busk 1884
<i>Orthoporidae</i>						
<i>O. erectus</i>	Magellan Straits	55°S	72°W	320	(+7.8)	BMNH
<i>O. erectus</i>	Montevideo	37°17'S	53°54'W	1100	+2.8	BMNH
<i>O. erectus</i>	Is. Innocentes	50°33'S	74°53'W	150		Moyano 1974
<i>O. erectus</i>	Is. Topar	50°8.5'S	74°41'W	360		Moyano 1974
<i>O. erectus</i>	Canal Zenteno	52°49'W	73°40'S	30-40		Moyano 1974
<i>O. aff. erectus</i>	E. Falkland Is.	52°09'S	58°14'W	79	+8.3	BMNH
<i>O. aff. erectus</i>	E. Falkland Is.	50°29'S	58°52'W	140	+4.78	BMNH
<i>O. aff. erectus</i>	E. Falkland Is.	50°30'S	58°19'W	141	+5.4	BMNH
<i>O. aff. erectus</i>	E. Falkland Is.	52°31'S	58°29'W	146	+5.45	BMNH
<i>O. aff. erectus</i>	E. Falkland Is.	50°50'S	57°13'W	144	+5.61	BMNH
<i>O. robusta</i>	Chile	37°37'S	73°40'W	600		Moyano 1981

number, opercular variation etc., should result in a better understanding of the systematic relationships within the Lekythoporidae, and the relationships of the family with other ascophoran groups.

LEKYTHOPORA MacGillivray

Lekythopora MacGillivray, 1883 : 194.

TYPE SPECIES. *L. hystrix* MacGillivray.

DESCRIPTION. Colonies forming short, irregularly cylindrical branches. Zooids with several series of frontal septulae. Primary orifice sinuate, operculum extended proximally but not distinctly sinuate. Ovicells with a frontal, marginally porous area covered by cuticle.

REMARKS. *L. hystrix* appears to be the only species referable to the genus. Harmer (1957 : 884) referred *Phylactella lucida* Hincks to *Lekythopora*; this species has been discussed by Cook (1968 : 220) and referred to *Celleporina*. *L. perplexa* Harmer (1957 : 884, pl. 59, figs. 5–7, 10) is also a 'celleporine' species with 'normal' frontal budding and tabulate ovicells and may be provisionally referred to *Celleporina*. Harmer (1957 : 885) also mentioned an unnamed species of *Lekythopora* from Japan. Examination of his specimens shows that these colonies, too, are referable to *Celleporina*. *L. laciniosa* Calvet (1907 : 445, pl. 29, figs. 13, 14) is attributable to *Celleporina*.

Lekythopora hystrix MacGillivray

Lekythopora hystrix MacGillivray, 1883 : 194, pl. 2, figs. 6, 6a–d; 1885 : 113, pl. 2, fig. 6; 1888 : 201, pl. 156, figs. 4–10; 1895 : 106, pl. 14, figs. 1–2. Waters, 1885 : 308. Brown, 1958 : 83.

Lekythopora avicularis Maplestone, 1909 : 273, pl. 78, fig. 12.

SPECIMENS EXAMINED. BMNH, Port Phillip Heads, Victoria, 1897.5.1.934, 937, 1899.5.1.1328, 1934.10.20.103. Port Western, S. Australia, 1934.2.20.23. Australia, 1883. 10.15.125–145. Port Jackson, Sydney, 1981.4.1.1. NMV, Port Phillip Heads 64611, 64612 (fig'd MacGillivray, 1888) and 64602.

DESCRIPTION (Figs. 14a, 15). Primary zooids with short peristomes, frontally budded zooids with long, curved peristomes, directed peripherally, sometimes with a secondary, topographically proximal, sinus. Peristomal avicularia with curved, acute rostra, placed on the edge of the peristome. Interzooidal avicularia elongated, only slightly expanded and rounded terminally, orientated proximally to branch growth. Ovicell with frontal area surrounded by minute pores.

REMARKS. MacGillivray (1888 : 211) noted that the primary orifice was difficult to see, and described it variously as 'rounded' (1883) or 'with a notch in the lower lip' (1888). In one illustration (1885, pl. 2, fig. 6), he actually figured the relationship of the proximal sinus with a distally placed ovicell, but apparently did not notice that this orientation was in contradiction to his description of the ovicell as 'proximal'. However, he was aware of the reversal of orifice orientation with respect to direction of growth in *P. anomala*, and compared it with that of *L. hystrix*. The relationships of *L. mooraboolensis* Maplestone (1902 : 25, pl. 2, fig. 18) and *L. kitsoni* Maplestone (1902 : 25, pl. 2, fig. 19), from the Australian Tertiary, are difficult to evaluate without specimens. *L. mooraboolensis* was described from a single, small, globular specimen of 3–4 zooids and may have been the young astogenetic stage of a colony of *Conescharrellina*. *L. kitsoni* was described as ligulate and bilaminar and appears to have had 'proximal' ovicells with a frontal area. It may be assignable to either *L. hystrix* or *P. anomala* (see below).

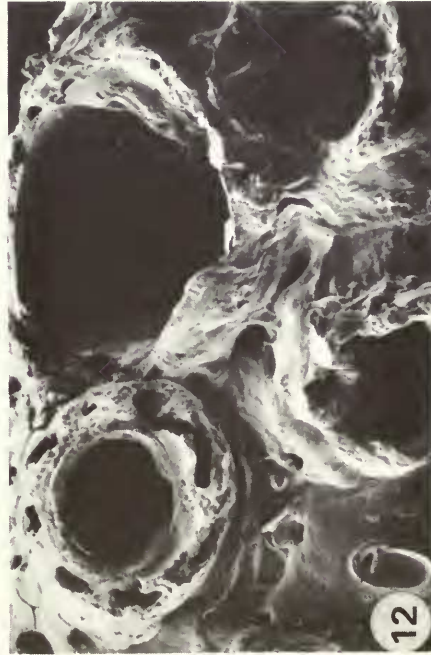
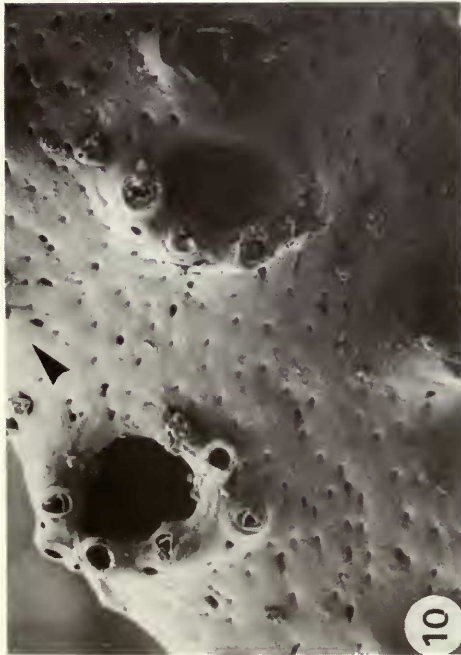
Apart from *L. kitsoni*, *L. hystrix* is apparently the only species of the family which has a fossil record. Both Waters (1885) and MacGillivray (1895) noted its occurrence from several Tertiary Australian localities (see also Brown, 1958).

POECILOPORA MacGillivray

Poecilopora MacGillivray, 1886 : 136.

TYPE SPECIES. *P. anomala* MacGillivray.

DESCRIPTION. Colonies with compressed, cylindrical, or 'bilaminar' branches, bifurcating in one plane. Zooids in opposing interdigitating series. Primary orifice sinuate, operculum extended proximally but not sinuate. Ovicells with a frontal area covered by cuticle, visible late in ontogeny.



Figs 10–13 Scanning electron micrographs of orifices of Lekythoporidae; arrows indicate direction of colony growth: (10) *Turritigera stellata* (Busk) BMNH 1897.12.9.520B, Montevideo, secondary orifices with terminal peristomial avicularia $\times 70$; (11) *T. reticulata* sp. nov. BMNH 1890.4.16.2A, Marion Island, primary orifices and developing ovicell $\times 80$; (12) *Poecilopora anomala* MacGillivray BMNH 1888.11.14.291, Port Phillip Heads, interdigitating, opposing zooid series at growing edge, showing primary orifices $\times 130$; (13) *P. anomala* secondary orifices, showing elongated marginal peristome, immersed central peristomes, peristomial and interzooidal avicularia $\times 80$.

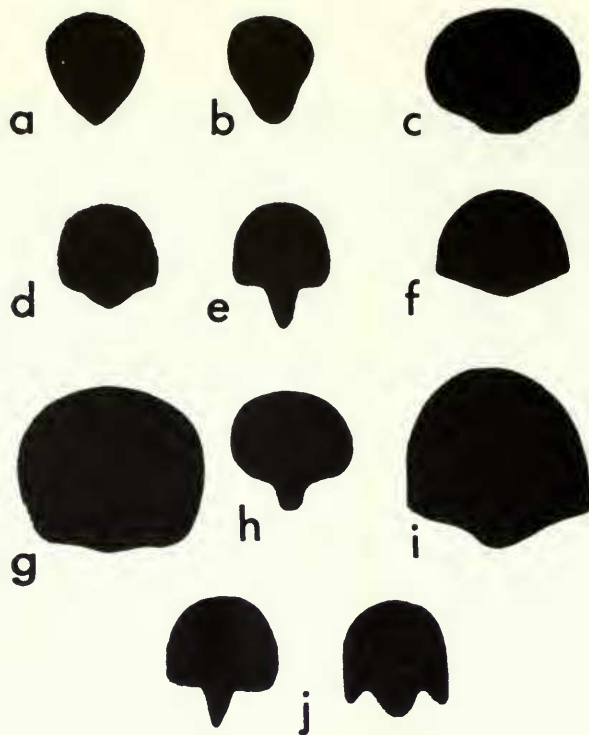


Fig. 14 Silhouettes of opercula of Lekythoporidae and Orthoporidroides. Scale bar = 0.50 mm; (a) *Lekythopora hystrix*; (b) *Poecilopora cribritheca*; (c) *Turritigera stellata*; (d) *T. reticulata*; (e) *T. fenestella*; (f) *Catadysis immersum*; (g) *Orthoporidra compacta*; (h) *O. petiolatus*; (i) *O. solida*; (j) *Orthoporidroides erectus*.

Poecilopora anomala MacGillivray

Poecilopora anomala MacGillivray, 1886 : 136, p. 1, fig. 9; 1888 : 211 (as *P. anomala*), pl. 156, figs. 11–13.

?*Turritigera stellata* Thornely (not Busk), 1924 : 18.

SPECIMENS EXAMINED. BMNH, Port Phillip Heads, 1887.12.10.67, 1888.11.14.103, 134, 291, 1897.5.1.947, 948, 949, 1889.7.1.3613. Port Western, South Australia, 1899.7.1.5129. Challenger Stn. 163A, Twofold Bay, New South Wales, 220 m, 1899.7.1.4081, 1963.2.12.15.

DESCRIPTION (Figs. 3, 12, 13) The small colonies rarely exceed a height of 10 mm, and are branched in one plane. The 'bilaminar' growth resembles that of *Flabellopora*. The primary orifice has an indistinct sinus proximally. Zooids small, with porcellaneous frontal shields with scattered septulae. Peristomes long at lateral margins of colony, flaring terminally; short elsewhere, with one acute avicularium. Interzooidal avicularia short, slightly expanded, and rounded terminally, randomly orientated. Ovicells prominent even late in ontogeny, protruding beyond the secondary thickening, frontal area surrounded by minute pores.

REMARKS. The early stages of the colony may consist of the ancestrula and one encrusting zooid generation only (1899.7.1.3613).

MacGillivray (1886 : 137) noted that the reversal of orifice orientation was the explanation for the apparently 'proximal' ovicells, and postulated that *L. hystrix* might have a similar structure.

Thornely's (1924) record of '*Turritigera stellata*' was not from an Antarctic locality. Although most of the stations mentioned in her paper were from Wilkes Land, Antarctica,

the locality 'Maria Island' (42°37'S, 148°E, 73 m) is Tasmanian (see Livingstone, 1928 : 8). Thornely noted that her colonies were 'bilaminar', that the zooids had tubular peristomes with only one marginal avicularium, and that the ovicells had a perforated frontal area. The locality of her specimens indicates that they were either *L. hystrix* or *P. anomala*, and the colony form suggests strongly that they were the latter.

The specimens from *Challenger* Stn 163A were not described by Busk (1884). The other bryozoans from this Station include a large number of cellariiform and cellulariiform species, which provide substrata for the colonies of *P. anomala*.

***Poecilopora cribritheca* (Harmer)**

Catadysis cribritheca Harmer, 1957 : 886, pl. 59, figs 9, 12–15, 22, 23.

SPECIMENS EXAMINED. ZMA, LECTOTYPE, Siboga Stn 105, Sulu Archipelago, 275 m. BMNH, Paralectotype, as above, 1981.5.6.1.

DESCRIPTION (Fig. 14b). Colonies with compressed cylindrical branches. Primary orifice with a wide sinus. Zooids with porcellanous calcification and scattered frontal septulae. Peristomial avicularia not protuberant, rounded or subtriangular. Ovicell immersed, but the frontal area, which has minute, slit-like pores, remains visible.

REMARKS. Harmer (1957) assigned *P. cribritheca* to *Catadysis*, which has cylindrical branches of zooids without long peristomes but with numerous frontal pores. The porcellanous calcification, compressed branches, long peristomes and exposed frontal area of the ovicells of *P. cribritheca* are all characters typical of *Poecilopora*.

P. cribritheca differs from *P. anomala* in its slightly larger zooids, and the shape and distribution of the avicularia. Interzooidal avicularia seem to be absent, but the material is fragmentary, and incomplete. *P. cribritheca* is the only species of Lekythoporidae known to occur in the tropical waters of the Northern hemisphere, but is from fairly deep water (275 m) near the equator.

***TURRITIGERA* Busk**

Turritigera Busk, 1884 : 129.

TYPE SPECIES. *T. stellata* Busk.

DESCRIPTION. Colonies with cylindrical branches, sometimes becoming reticulate with anastomoses. Most zooids curved so that their peristomes open on one side of the branch. Branches dichotomous or formed by frontally budded zooids arising in groups at right angles to the primary branch, in more than one plane. Primary orifice sinuate, but operculum curved or sinuate proximally. Peristomial avicularia sometimes numerous, occurring on the edge of peristomes, often on raised processes. Ovicell rapidly occluded by secondary calcification, but often remaining prominent.

***Turritigera stellata* Busk**

Turritigera stellata Busk, 1884 : 130, pl. 24, fig. 1. Waters, 1888 : 22, pl. 1, figs. 22, 25; 1904 : 76, pl. 5, fig. 3, pl. 8, fig. 13; 1905 : 242, pl. 29, figs. 19, 20. Moyano, 1974 : 18, figs. 4, 8, 31–34. not *Turritigera stellata* Thornely 1924, see *P. anomala*.

SPECIMENS EXAMINED. BMNH, *Challenger* Stn. 320, 1100 m, 1887.12.9.517.520B, 1899.7.1.3166,3167, 1944.1.8.240,241. *Challenger* Stn. 142, 275 m, 1887.12.9.518,519, 1899.7.1.498,499,500, 1934.2.16.13, 1944.1.8.239,242. Locality? New Zealand, 1936.12.30.155.

MM, *Challenger* Stn. 320, T38–40; Expedition Antarctic Belge, T17–37.

DESCRIPTION (Figs. 4, 10, 14c). Colonies reaching a height of 20–30 mm, branched irregularly. Primary orifice with a small, rounded proximal sinus, operculum with a distal flange, curved proximally. Zooids with numerous frontal septulae, which become slit-like as

calcification increases. Peristomes long, flaring terminally, with one to seven terminal avicularia, which are sometimes raised on short processes. Mandibles and rostra acute. Interzooidal avicularia elongated, slightly expanded and rounded terminally, randomly orientated, sometimes present on non-zooidal 'basal' side of colony. Ovicell with a small frontal area which is rapidly obscured by frontal thickening. 18 tentacles (Waters). 'Basal' thickening extrazoooidal, with slit-like pores and minute avicularia.

REMARKS. The South American (Stn. 320), South African (Stn. 142) and Antarctic populations show some differences in characters. Colonies from Stn. 320 are rather delicate, with numerous small peristomial avicularia, and interzooidal avicularia on the 'frontal' and 'basal' sides. There is relatively little extrazoooidal thickening (see also Moyano, 1974). Colonies from Stn. 142 are at a later stage of ontogenetic development and consist of astogenetically earlier fragments. They appear more robust, with considerable 'basal' and 'frontal' thickening. The axially directed, proximal, peristomial avicularium is large and the remainder are reduced in number, usually to two or three. Interzooidal avicularia are absent. Colonies from Waters's (1904) Antarctic Stations are very robust, and the zooids tend to be arranged biserially (c.f. *T. reticulata*). Waters noted that some colonies possessed anastomoses (1904, pl. 5, fig. 3a). The zooids have numerous peristomial avicularia, but interzooidal avicularia are very rare. In contrast, specimens from ?New Zealand (locality doubtful) are delicate but have one enlarged peristomial avicularium, like those from South Africa. *T. stellata* would therefore appear to be a very variable species. The extent and significance of this variation can only be assessed when complete colonies, showing all astogenetic and ontogenetic stages can be compared from a wide range of populations. Recently, for example, d'Hondt (1981 : 41, pl. 5, figs. 1-3) has described a new, abyssal form, *T. spectabilis*, from a depth range of 1661-4402 m, off Uruguay. *T. spectabilis* resembles some forms of *T. stellata* in having only one, large peristomial avicularium. Ovicells were absent.

The operculum of *T. stellata* figured by Waters (1904, pl. 5, fig. 3b) was distinctly sinuate, like the primary orifice. Waters's preparation of opercula (MM T33) is badly preserved and no sinus is visible. None of the numerous opercula in the Busk preparations from South African material (BMNH 1899.7.1.498,499) shows any sinus.

Turritigera reticulata sp. nov.

SPECIMENS EXAMINED. BMNH, HOLOTYPE and Paratypes, all parts of one colony, Marion Island, 1890.4.16.2A.

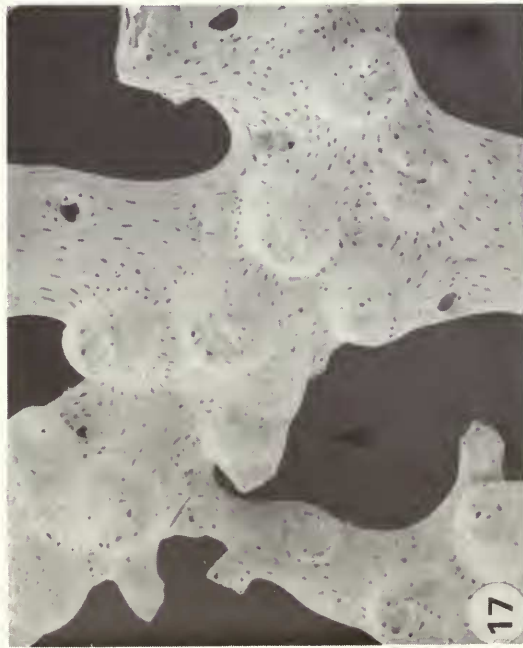
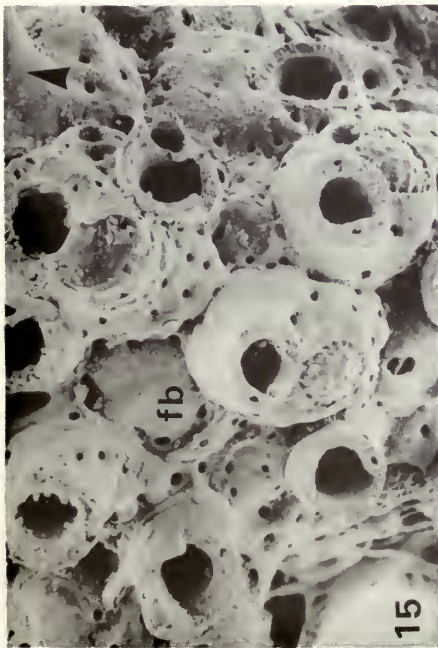
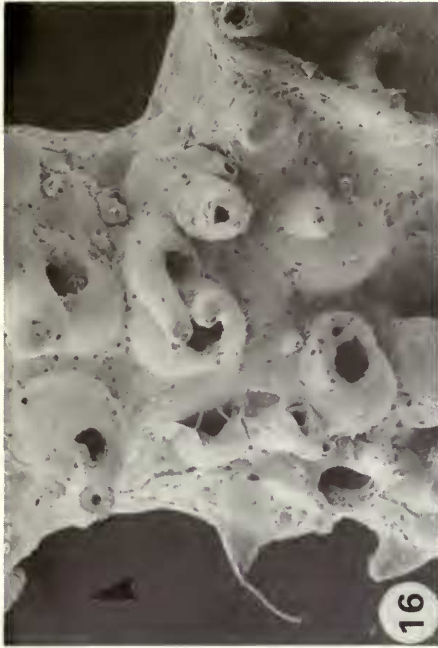
ETYMOLOGY. *Reticulatus* (L)—net-like, referring to the colony form.

DESCRIPTION (Figs. 8, 11, 14d, 17, 18). Colonies large, 50 mm in height, reticulate, with anastomosing branches. Zooids very large, alternating and biserial, peristomes short. Primary orifice very small, with a fairly wide sinus, operculum distinctly sinuate. Secondary orifice often forming a topographically proximal sinus. Frontal pores numerous, becoming slit-like. Peristomial avicularia small, one to three are borne on a stout suboral, topographically distal process, mandibles short, triangular. Interzooidal avicularia absent. Ovicells very large, with marginal pores; prominent at first, becoming partially obscured by extrazoooidal thickening, often orientated medially.

REMARKS. The reticulate growth form of *T. reticulata* is shared by *T. fenestella* (see below) and, according to Waters (1904), by some colonies of *T. stellata*. The large zooidal dimensions of *T. reticulata*, together with its very small primary orifice distinguish it from *T. fenestella*.

Turritigera fenestella sp. nov.

SPECIMENS EXAMINED. BMNH, HOLOTYPE and Paratypes, all parts of one colony, Marion Island, 1890.4.16.2B.



Figs 15–18 Scanning electron micrographs of Lekythoporidae; arrows indicate direction of colony growth: (15) *Lekythopora hystrix* MacGillivray BMNH 1883.10.15.125–145, Australia, zooids with topographically proximal ovicells, note developing frontal bud (fb) $\times 55$; (16) *Turritigera fenestella* sp. nov. BMNH 1890.4.16.2B, Marion Island, zooids with ovicells, note median and lateral orientation $\times 36$; (17) *T. reticulata* sp. nov. BMNH 1890.4.16.2A, Marion Island, part of colony from 'frontal' side showing anastomosis, note early closure of ovicelled zooids $\times 20$; (18) *T. reticulata*, zooids showing relatively late ovicell development, and secondary (topographically proximal) 'sinus' (small arrows) $\times 37$.

ETYMOLOGY. *Fenestella* (L)—a little window, referring to the colony form.

DESCRIPTION (Figs. 9, 14e, 16). Colony large, 50 mm in height, reticulate, with anastomosing branches. Zooids irregularly arranged, fairly small, with a primary orifice with a proximal plate, in which there is a distinct round sinus; operculum also with a distinct sinus. Frontal pores fairly numerous, rounded, becoming obscured. Peristomial avicularia one to three, one borne on a very long, curved suboral process. Mandibles triangular, the suboral mandible large, rostrum hooked terminally. Ovicells small, smooth, remaining prominent, although obscured by extrazoooidal thickening, often orientated medially.

REMARKS. The similarities in colony form of *T. fenestella* and *T. reticulata*, which were from the same locality, tend to obscure the distinct differences in budding pattern, zooidal size and orificial characters which exist between them. The zooids of *T. fenestella* are similar in size to those of *T. stellata*, but differ completely in the form of the avicularian processes and in the shape of the operculum. The three species described above form a complex, which requires more plentiful material for elucidation.

CATADYSIS Canu & Bassler

Catadysis Canu & Bassler, 1927 : 12, 23, 25.

TYPE SPECIES. *Myriozoum immersum* Busk (= *Schizoporella challengeria* Waters).

DESCRIPTION. Colonies with regularly cylindrical branches, zooids opening on all sides. Zooids with numerous frontal septulae, peristomes not prominent. Primary orifice with a rounded sinus, operculum curved proximally. Peristomial avicularia small, interzooidal avicularia absent. Ovicells imperforate.

***Catadysis immersum* (Busk)**

Myriozoum immersum Busk, 1884 : 170, p. 25, fig. 4.

Schizoporella challengeria Waters, 1888 : 30, pl. 2, figs. 25–28.

Catadysis challengeria (Waters) Canu & Bassler, 1927 : 11, Bassler, 1953 : G233.

Catadysis immersum (Busk) Harmer, 1957 : 885. Hayward, 1980 : 712, figs. 5A–D.

SPECIMENS EXAMINED. BMNH, *Challenger* Stn 320, 1100m, 1887.12.9.683,684,685B, 1899.12.12.18, 1899.7.1.2295, 1934.11.12.57, 1944.1.8.333,334, 1963.2.12.221,247. 'Bruce' Stn 346 (Scottish National Antarctic Expedition) Burdwood Bank, 1936.12.30.297.

DESCRIPTION (Figs. 2, 6, 7, 14f). Colonies large, 50 × 30 mm, branching in all planes. Zooids with numerous frontal septulae which become immersed by extrazoooidal calcification as a series of slit-like pores. Branches cylindrical, smooth, composed of four series of zooids. Peristomes never prominent, orifices rapidly obscured by secondary calcification, leaving rounded pits on the branch surface. Peristomial avicularia small, proximal and distal, mandibles triangular. Ovicells obscured very early in ontogeny.

REMARKS. Waters (1888) introduced the name '*Schizoporella challengeria*' for Busk's species because he considered that it belonged to the genus *Schizoporella* and that the combination was therefore preoccupied by *Onchopora immersa* Haswell (1880), which he also assigned to *Schizoporella*. *O. immersa* is referable to the genus *Tetraplaria* (see Harmer, 1957 : 1055), and as *Catadysis* has little in common with *Schizoporella*, Waters's name '*challengeria*' is unnecessary (see also Harmer, 1957 : 885, and Hayward, 1980).

Most specimens are small and fragmentary, but one from *Challenger* Stn 320 exceeds 50 mm in width, with numerous branches.

ORTHOPORIDRA Canu & Bassler

Orthopora Waters, 1904 (preoccupied).

Orthoporidra Canu & Bassler, 1927 : 12, 23, 34.

TYPE SPECIES. *Orthopora compacta* Waters.

DESCRIPTION. Colony with irregularly cylindrical branches. Primary orifice usually straight proximally, but opercula may be curved. Zooids with numerous frontal septulae, calcification smooth and very thick. Peristomial avicularia often raised on long, hollow mucronate prominences. Ovicells large, usually imperforate, but with small frontal avicularia.

REMARKS. A large number of specimens has been recorded from many Antarctic and sub-Antarctic localities. These appear to have the general character of *O. compacta* as described below. Small differences in the primary orifice and operculum, however, indicate that population studies are necessary, and it is possible that several distinct species will be found to exist, once plentiful material has been examined.

Orthoporidra compacta (Waters)

Orthopora compacta Waters, 1904 : 75, pl. 5, figs. 4a-i. ?Redier, 1965 : 4, 32.

Orthoporidra compacta: Canu & Bassler, 1927 : 12; 1929 : 515, fig. 214. Rogick, 1965 : 406. Moyano, 1978 : 44.

?*Cellepora setosa* Thornely, 1924 : 17, fig. 5. Livingstone, 1928 : 76, pl. 3, fig. 8, Figs. 18-20. Moyano, 1978 : 44.

?not *Cellepora setosa*: Redier, 1965 : 30; 1966 : 2.

SPECIMENS EXAMINED. MM, T10-15, 343, Waters's (1904) preparations including operculum (T14) and tentacles (T12), Expedition Antarctique Belge. BMNH, Halley Bay, 1966.3.4.4. Bahia, Chile, 1971.3.26.29. Scotia Bay, S. Orkneys, 1920.12.11.3. McMurdo Sound, 1981.3.1.1.

DESCRIPTION (Figs. 14g, 21, 22). Colonies large, branched in several planes. Primary orifice and operculum slightly curved proximally. Zooids large, frontal septulae distinct, marginal and circum-oral, in two rows across exposed frontal shield. Suboral, topographically distal, avicularium raised on a long tubular process, mandible rounded or triangular, rostrum bar with a ligula. Interzooidal avicularia oval or expanded terminally, rostrum bar with a ligula, usually orientated proximally. Ovicell large with small avicularia on the surface. 24 tentacles (Waters).

REMARKS. The only type material consists of decalcified sections and preparations etc. The operculum (T14) differs from that figured by Waters (1904) and resembles that of *O. solida* in being slightly curved proximally, with lateral proximal lacunae which may be muscle insertions (cf. Waters, 1904).

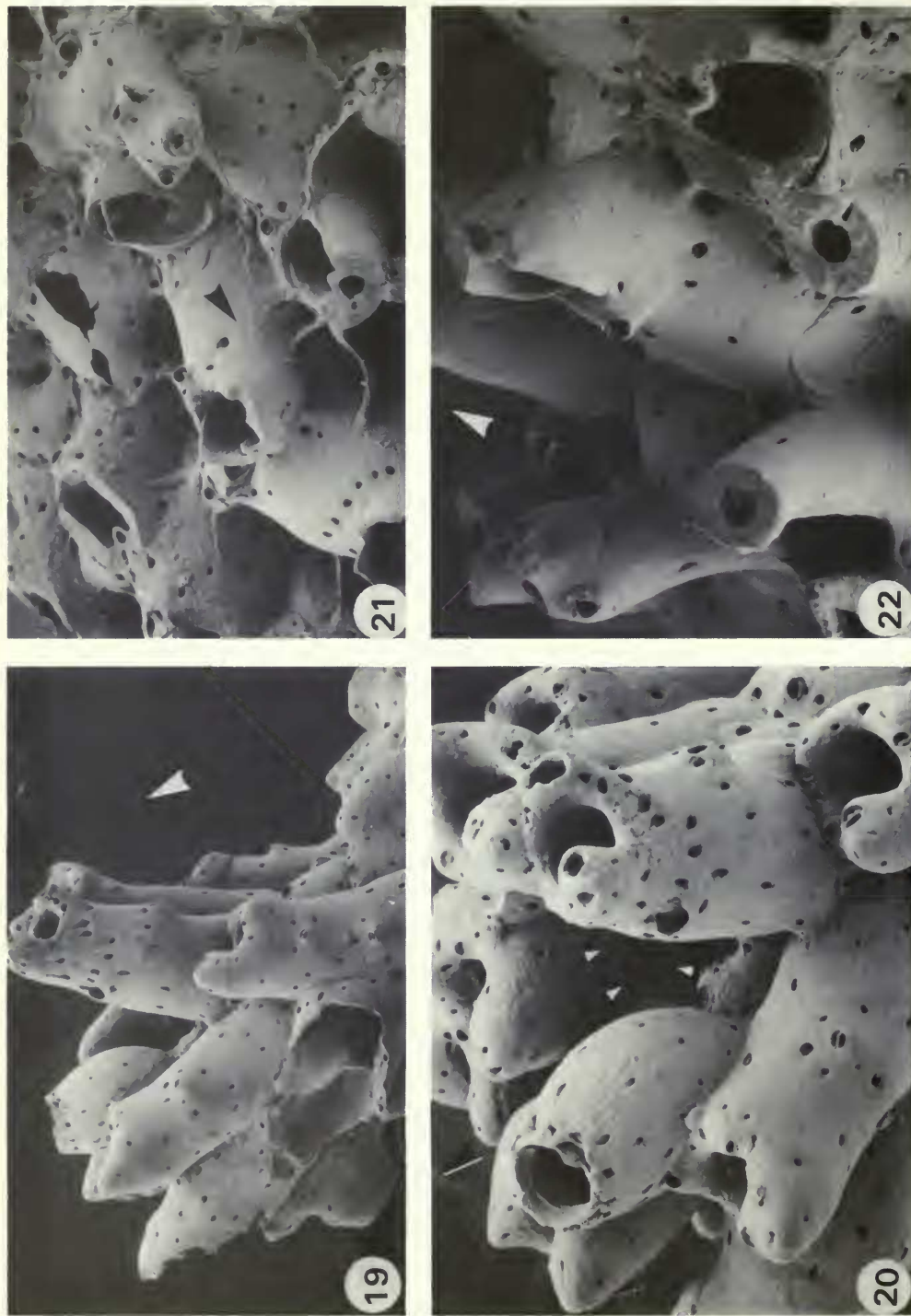
Thornely (1924) introduced *C. setosa* for specimens from several Antarctic localities. Her specimens were redescribed by Livingstone (1928), who noted that neither the primary orifice nor operculum were sinuate. Both authors figured large ovicells with small pores, or avicularia?, on their surfaces.

The only available specimen named as *O. setosa*, which is part of the material described or listed by Redier (1965, 1966), is a bifurcated branch from Antarctica identified by Dr A. B. Hastings (Stn 136, Expedition Antarctique Belge, BMNH 1964.8.2.5.). Although similar to *O. compacta* in most characters including those of the large, wide, ligulate interzooidal avicularia, this specimen differs in the dimensions of the orifice and in possessing a sinuate operculum. The primary orifice is straight proximally but has a small central notch, is longer than wide and generally far smaller than that of *O. compacta*. '*C. setosa* Redier' is therefore, in part at least, a separate taxon from *C. setosa* Thornely and *O. compacta*.

Additional material is required before all the Antarctic records of these forms can be reassessed. Redier's (1965) material of *O. compacta* also requires re-examination. His record of the Philippine Islands as a locality for the species is a mistaken reference to the illustrations included by Canu & Bassler (1929) in their paper on Philippine bryozoans.

Orthoporidra solida (Busk)

Cellepora solida Busk, 1884 : 200, pl. 29, fig. 12. Waters, 1904 : 76, pl. 5, fig. 5.



Figs 19–22 Scanning electron micrographs of *Orthoporidra*; arrows indicate direction of colony growth; (19) *O. solida* (Busk) BMNH 1899.7.1.3525, S.W. Australia, tip of branch $\times 30$; (20) *O. solida*, zooids with peristomial avicularia, central budding area (small arrows) $\times 50$; (21) *O. compacta* (Waters) BMNH 1966.3.4.4, Halley Bay, Antarctica, zooids showing secondary frontal buds and interzoooidal avicularium with ligulate bar $\times 50$; (22) *O. compacta*, peristomial processes with avicularia, note thickness of frontal shield $\times 71$.

SPECIMENS EXAMINED. BMNH, LECTOTYPE (chosen here), *Challenger* Stn 160, 4758m. 1899.7.1.3525, the specimen figured by Busk, 1884. Paralectotypes 1887.12.9.775-777; 1899.7.1.3526.

DESCRIPTION (Figs. 5, 14i, 19, 20). *Orthoporida* with very large zooids, with numerous, scattered frontal septulae. Primary orifice and operculum curved proximally. Peristome not very prominent. Peristomial avicularia proximal and paired, lateral, raised on blunt mucros, mandibles rounded, rostra subtriangular. Interzooidal avicularia oval, large. Ovicells large, with small avicularia and scattered pores.

REMARKS. The colonies form branched cylindrical masses 5-10 mm in height. Secondary thickening is less developed than in *O. compacta*, and consists of numerous kenozooids as well as extrazooidal tissue. The avicularian processes are short and blunt, quite unlike those of *O. compacta*.

Busk (1884: 200, pl. 29, fig. 12a) described the large interzooidal avicularia (as 'operculum' in the explanation of Plate 29), and Waters (1904, pl. 5, Fig. 5) also illustrated an operculum. The preparations in the BMNH show that the opercula are far larger than the dimensions indicated by Waters's figure.

Orthoporida petiolata (Waters)

Cellepora petiolata Waters 1904 : 76 (*nom. nud.*); 1905 : 241, pl. 29, figs. 19, 20.

Catadysis petiolata: Hayward, 1980 : 714, Figs 5 E-H.

SPECIMENS EXAMINED. MM, T2-T6, Expedition Antarctique Belge. BMNH, Houtjes Bay, S. Africa, 1936.12.30.300c. Stn 346, Scottish National Antarctic Expedition, Burdwood Bank, 1981.3.1.12.

DESCRIPTION (Fig. 14h). Colony arising from a minute thickened base of kenozooids, encrusting erect bryozoa, 10-15 mm in height. Zooids with marginal and circum-oral septulae. Primary orifice and operculum with a small sinus. Suboral peristomial avicularium raised on long processes, mandible small, rounded or elongated and triangular. Ovicells small, prominent at first, with frontal pores and small avicularia. 14 tentacles (Waters).

REMARKS. Waters (1904) mentioned that a species which he proposed to name '*C. petiolata*' was similar in character to *O. compacta*. In his formal introduction (1905) he gave no further details, and figured only the operculum and mandibles. Waters's preparation (T5) shows an operculum with a small rounded sinus.

The generic assignment of *O. petiolata* is arbitrary. The official characters are similar to those of some species assigned here to *Turritigera* (e.g. *T. fenestella*), and to *Catadysis immersum* (see Hayward, 1980). The budding pattern of the zooids, and the distribution of the frontal septulae resemble those of *Orthoporida compacta*.

Comparison of the Lekythoporidae with the genus *Orthoporidroides* Moyano

Frontally budded zooids with cryptocystidean frontal shields, which form massive or cylindrical, erect branches are typical of the Family Celleporinidae Harmer. Genera such as *Turbicellepora* (see Hayward, 1978) and *Celleporina* (see Harmer, 1957) also have oral avicularia derived from circum-oral frontal septulae, and often have elongated peristomes with terminal avicularia. Large, interzooidal (vicarious) frontally budded avicularia, and ovicells with porous frontal areas (tabulae) are also typical of these genera. The genera included in the Lekythoporidae are therefore distinguished from those in the Celleporinidae principally by their 'reversed' frontal budding pattern. The apparent close similarity between the Families is illustrated by *Orthoporidroides erectus* (Waters).

CELLEPORINIDAE Harmer

Celleporinidae Harmer, 1957 : 899.

ORTHOPORIDROIDES Moyano

Orthoporidroides Moyano, 1974 : 201. 1981.

TYPE SPECIES. *Cellepora armata* var. *erecta* Waters.

***Orthoporidroides erectus* (Waters)**

Cellepora armata var. *erecta* Waters, 1888 : 36. pl. 3, figs 4, 41, 43.

Orthoporidroides erectus : Moyano, 1974 : 21, Figs. 6, 35–40.

SPECIMENS EXAMINED. BMNH, *Challenger* Stn 308, 320m, 1889.12.12.7. *Challenger* Stn 320. 1100m. 1888.3.14.3, 1899.7.1.3584, 3587, 3592, 3602, 3606; 1934.11.12.5. Shackleton-Rowett Exped., ?S. Orkney, 1923.12.1.39,48.

DESCRIPTION (Fig. 14j). Colonies erect, branching, arising from a small, encrusting base. Zooids budded frontally and distally, primary orifice with a shallow sinus directed towards the outside of the branch, operculum produced into a triangular sinus. Avicularia suboral, terminal on a long, proximally produced peristome, mandible acute. Ovicell hyperstomial, with a small, frontal slit.

REMARKS. Moyano (1974) has illustrated the morphology of *O. erectus* fully and compared it with that of *Turritigera stellata*. Moyano also noted similarities between *O. erectus* and *Cellepora petiolata* Waters (1905), see above. The opercula of *O. erectus* figured by Moyano resemble those illustrated by Waters, but differ slightly from those of the specimens from *Challenger* Stn 320, which are very variable (Fig. 14j). These specimens were not described by Busk (1884) or Waters (1888).

Discussion

Study of the relationships of the ovicell in the Lekythoporidae illustrates the importance of analysis of the astogenetic structure of colonies, as well as the ontogeny of their member zooids. It is interesting that since the ovicells of these genera were first described as 'proximal' in position, this monothetic 'character' has been accepted almost without question, and has even been modified (e.g. Harmer, 1957 : 884) in an attempt to include other taxa in the family, a frequent occurrence in bryozoan taxonomy (see Boardman *et al.*, 1969). The explanation of the unusual relationships of the ovicell has awaited first, the demonstration of frontal budding by Banta (1972) and second, the realisation that in both erect and rooted colonies, this type of astogeny may include reversal of zooidal orientation with respect to the direction of colony growth (see Cook & Lagaaij, 1976, and Cook & Chimonides, 1981).

The similarities in several characters among the genera assigned to the Lekythoporidae and Celleporinidae suggest a close relationship between the families.

It is possible that parallel complexes exist, each containing groups of species with totally different budding patterns, but with similar zooidal characters and even with similar resultant colony forms. *Orthoporidroides robusta* Moyano (1981 : 182, Figs 1–7), for example, resembles some other, unnamed Recent specimens from the Falkland Islands (BMNH, 1981.3.1.6,9,10) in illustrating how the type of budding pattern found in *O. erectus* may have been transformed into the type found in the Lekythoporidae. Colonies of both species are large, maximum height 50–60 mm, and profusely branched, with a range of zooid orientations. In *Orthoporidroides* sp. there are several sequential series of outwardly directed interzooidal, frontally budded zooids. The more centrally placed zooids of branches, which are those budded earlier in the astogenetic sequence, tend to have 'reversed' orientation of orifices, while the more numerous peripheral zooids have a 'normal' orientation. Some intermediate orientations, and ovicells in a 'proximal', lateral and distal topographical position occur in both *O. robusta* and the unnamed species. This differs from *O. robusta* in

its orifice shape, which has a very long, narrow sinus, and the number of peripheral zooids in its branches.

At present it is difficult to determine whether or not astogeny and structure reflect closer genetic links than those of zooidal morphology. In order to trace possible changes in, for example, zooidal orientation and astogeny with time, a range of fossil specimens is necessary. Colonies of Lekythoporidae are robust enough to be preserved in fossil sediments; unfortunately only *L. hystrix* is unequivocally known to have a fossil record. Lack of records of other species, both in Recent and fossil deposits, is probably caused by difficulties of recognition, due to the small size of the colonies, and rapid thickening of extrazoooidal calcification, which obscures the zooidal features. Recent species tend to inhabit the deeper shelf waters, and until more collections from these regions, particularly from high latitudes in the Southern hemisphere become available, detailed analysis of colonies is not possible.

Although the characters of the type-species of the five genera of Lekythoporidae are distinct, several of the other species described here show intermediate sets of correlations which make generic assignment somewhat arbitrary.

The 'easily recognised' character of the 'proximal ovicell' has to a great extent obscured analysis of other structures in the past. The fragmentary nature of most of the type material requires amplification by well preserved, complete colonies before the range of astogenetic, ontogenetic, polymorphic and microenvironmental variation of the taxa can be analysed and described.

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References

- Banta, W. C. 1972. The body wall of cheilostome Bryozoa V. Frontal budding in *Schizoporella unicornis floridana*. *Mar. Biol. Berlin* **14** (1): 63–71.
- Bassler, R. S. 1953. In R. C. Moore. *Treatise on Invertebrate Paleontology*. Part G. Bryozoa. Lawrence, Kansas.
- Boardman, R. S. & Cheetham, A. H. 1973. Degrees of colony dominance in stenolaemate and gymnolaemate Bryozoa. In R. S. Boardman, A. H. Cheetham & W. A. Oliver. *Animal Colonies*. Stroudsburg.
- Boardman, R. S., Cheetham, A. H. & Cook, P. L. 1969. Intracolony variation and the genus concept in Bryozoa. *Proc. N. Am. Paleont. Conv.* 1969, Part C: 294–320.
- Brown, D. A. 1958. Fossil cheilostomatous Polyzoa from South-West Victoria. *Mem. geol. Surv. Vict.* **20**: 1–90.
- Busk, G. 1884. Report on the Polyzoa, the Cheilostomata. *Rep. Voy. Chall. Exp. Zool.* **10** (30): i–xxiii, 1–216.
- Calvet, L. 1907. Bryozoaires. *Exped. Scient. 'Travailleur' et 'Talisman' 1880–1883*. **7**: 355–495.
- Canu, F. & Bassler, R. S. 1927. Classification of the Cheilostomatous Bryozoa. *Proc. U.S. natn. Mus.* **69** (14): 1–42.
- 1929. Bryozoa of the Philippine region. *Bull. U.S. natn. Mus.* **100** (9): i–xi, 1–685.
- Cook, P. L. 1968. Bryozoa (Polyzoa) from the coasts of tropical West Africa. *Atlantide Rep.* **10**: 115–262.
- 1977. Early colony development in *Aetea* (Bryozoa). *Amer. Zool.* **17**: 55–61.
- 1979. Some problems in interpretation of heteromorphy and colony integration in Bryozoa. In G. P. Larwood & B. R. Rosen. *Biology and Systematics of Colonial Organisms*. Systematics Association Special Volume 13. London & New York.
- 1983. Bryozoa from Ghana—a preliminary survey. *Annls Mus. r. Afr. cent.* **8**, 235 Zool. (in press).
- Cook, P. L. & Chimonides, P. J. 1981. Morphology and systematics of some rooted cheilostome Bryozoa. *J. nat. Hist.* **15**: 97–134.

- Cook, P. L. & Lagaaij, R. 1976. Some Tertiary and Recent conescharelliniform Bryozoa. *Bull. Br. Mus. nat. Hist. (Zool.)* **29** (6): 317–376.
- Harmer, S. F. 1957. The Polyzoa of the Siboga Expedition. Pt. 4. Cheilostomata Ascophora II. *Siboga Exped.* **28d**: 641–1147.
- Haswell, W. A. 1881 (1880). On some Polyzoa from the Queensland coast. *Proc. Linn. Soc. N.S.W.* **5**: 33–44.
- Hayward, P. J. 1978. Systematic and morphological studies on some European species of *Turbicellepora* (Bryozoa, Cheilostomata). *J. nat. hist.* **12**: 551–590.
- 1980. Cheilostomata (Bryozoa) from the South Atlantic. *J. nat. Hist.* **14**: 701–722.
- d'Hondt, J.-L. 1981. Bryozoaires Cheilostomes bathyaux et abyssaux provenant des campagnes océanographique américaines (1969–1972) de l' "Atlantis II", du "Chain" et du "Knorr" (Woods Hole Oceanographic Institution). *Bull. Mus. natn. Hist. nat. Paris sér. 4*, **3** (A1): 5–71.
- Levinson, G. M. R. 1909. *Morphological and Systematic studies on the Cheilostomatous Bryozoa*. Copenhagen.
- Livingstone, A. A. 1928. The Bryozoa. Supplementary Report. *Scient. Rep. Australas. antarct. Exped.* **C9** (1): 1–93.
- MacGillivray, P. H. 1883. Descriptions of new or little known Polyzoa. Pt. 3. *Trans. Proc. R. Soc. Vict.* **19**: 191–195.
- 1885. Descriptions of new or little known Polyzoa. Pt. 8. *Trans. Proc. R. Soc. Vict.* **21**: 106–119.
- 1886. Descriptions of new or little known Polyzoa. Pt. 9. *Trans. Proc. R. Soc. Vict.* **22**: 128–139.
- 1888. Polyzoa. In F. McCoy. *Prodromus of the Zoology of Victoria*. Melbourne 1879–1890. Decade XVI: 209–220.
- 1895. A monograph of the Tertiary Polyzoa of Victoria. *Trans. R. Soc. Vict.* **4**: 1–166.
- Maplestone, C. M. 1902. Further descriptions of the Tertiary Polyzoa of Victoria. 8. *Proc. R. Soc. Vict. n.s.* **15** (1): 17–27.
- 1909. The results of deep-sea investigations in the Tasman Sea, 1. The expedition of M.M.C.S. 'Miner', 5. The Polyzoa. *Rec. Aust. Mus.* **7** (4): 267–273.
- Moyano, H. I. G. 1972. Aspectos sistematicos, astogeneticos y reproductivos de *Inversiula nutrix* Jullien 1888. *Boln. Soc. Biol. Concepcion* **45**: 105–116.
- 1974. Briozoos marinos Chilenos. II. Briozoos de Chile Austral, I. *Gayana Zool.* **30**: 3–41.
- 1978. Bryozoa de Bahías Antárticas: algunas aspectos ecológicos. *Serie Cient. Inst. antart. Chil.* **24**: 35–60.
- 1981. *Orthoporidroides* Moyano, 1974: consideraciones taxonomicas y decripcion de *Orthoporidroides robusta* sp. n. (Bryozoa, Cheilostomata). *Boln. Soc. Biol. Concepcion* **52**: 181–186.
- Murray, J. 1895. *A summary of the Scientific Results of the Challenger Expedition*. Part 1: xxxv–liii, 1–796; Part 2: vii–xxv, 797–1608. London, Edinburgh & Dublin.
- Nielsen, C. 1981. On morphology and reproduction of '*Hippodiplosia*' *insculpta* and *Fenestrulina malusii* (Bryozoa, Cheilostomata). *Ophelia* **20** (1): 91–125.
- Redier, L. 1965. Expéditions Antarctique Belges 1959–1960. Bryozoaires. *Bull. Inst. r. Sci. nat. Belg.* **41** (40): 1–39.
- Redier, L. 1966. Expéditions Antarctiques Belges 1964–1965. Bryozoaires (Suite). *Bull. Inst. r. Sci. nat. Belg.* **42** (25): 1–6.
- Rogick, M. D. Bryozoa of the Antarctic. 1965. In P. van Oye & J. van Meighen. *Biogeography and ecology in Antarctica. Monographiae biol.* **15**: 401–413.
- Silén, L. 1945. The main features of the development of the ovum, embryo and oecium in the oociferous Bryozoa Gymnolaemata. *Ark. Zool.* **35A** (17): 1–34.
- Thornely, L. R. 1924. Polyzoa. *Scient. Rep. Australas. antarct. Exped. C*, **6** (6): 1–23.
- Vigeland, I. 1952. Antarctic Bryozoa. *Scient. Results. Norw. Antarct. Exped.* **3** (34): 1–15.
- Waters, A. W. 1885. Chilostomatous Bryozoa from Aldinga and the River-Murray Cliffs, South Australia. *Q. Jl. geol. Soc. Lond.* **41**: 279–310.
- 1888. Supplementary Report on the Polyzoa. *Rep. Voy. Challenger Exp. Zool.* **31** (79): 1–41.
- 1904. Bryozoa. Result. Voyage S.Y. Belgica, Zoologie **4**: 1–114.
- 1905. Bryozoa from near Cape Horn. *J. Linn. Soc. Zool.* **29**: 230–251.